

- tion on population dynamics of Emperor Geese. *J. Wildl. Manage.* 61:191–201.
- SMITH, C. M., F. COOKE, G. J. ROBERTSON, R. I. GOUTIE, AND W. S. BOYD. 2000. Long-term pair bonds in Harlequin Ducks. *Condor* 102:201–205.
- TRUST, K. A., D. ESLER, B. R. WOODIN, AND J. J. STEGEMAN. 2000. Cytochrome P450 1A induction in sea ducks inhabiting nearshore areas of Prince William Sound, Alaska. *Marine Poll. Bull.* 40:397–403.
- VERMEER, K. 1983. Diet of the Harlequin Duck in the Strait of Georgia, British Columbia. *Murrelet* 64:54–57.
- WIENS, J. A., AND K. R. PARKER. 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. *Ecol. Appl.* 5:1069–1083.
- WOLFE, D. A., M. J. HAMEEDI, J. A. GALT, G. WATABAYASHI, J. SHORT, C. O'CLAIR, S. RICE, J. MICHEL, J. R. PAYNE, J. BRADDOCK, S. HANNA, AND D. SALE. 1994. The fate of the oil spilled from the *Exxon Valdez*. *Environ. Sci. Technol.* 28:561–568.

The Condor 102:926–929
© The Cooper Ornithological Society 2000

INFLUENCE OF FEMALE AGE AND BODY MASS ON BROOD AND DUCKLING SURVIVAL, NUMBER OF SURVIVING DUCKLINGS, AND BROOD MOVEMENTS IN REDHEADS¹

TINA YERKES²

Department of Zoology, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

Abstract. I documented brood and duckling survival, the number of surviving ducklings, and brood movements of Redheads, and examined the association between these variables and female age and body mass. Redhead brood success was 55% and duckling daily survival rates averaged 0.868. Female body mass, but not age, was related to brood and duckling survival and the number of surviving ducklings. Successful females were heavier and produced more ducklings. All brood-movement measures differed between successful and unsuccessful females, however, the distance of the first move between wetlands accounted for the most variability in brood success. Increased body mass, but not age, was associated with longer first brood movements.

Key words: *Aythya americana*, body mass, brood movements, brood survival, duckling survival, female age, Redhead.

Although North American Anatinae produce precocial young, females provide post-hatch care. Poor or reduced brood care may result in lower brood or duckling survival (Talent et al. 1983). Among ducks, several factors may affect individual variation in brood care: temporal variation, brood age and size, and adult

age and body mass. Older parents, as compared to yearlings, should maximize fitness by exhibiting greater parental investment (PI) (Trivers 1974). Older parents may also benefit from experience gained through raising previous broods, and thus have higher brood success than younger parents. Afton (1984) provided weak support for increased PI with age in Lesser Scaup (*Aythya affinis*) because the amount of time females spent in brood care increased with age to a point. Female age did not influence brood survival in Lesser Scaup (Afton 1984) or Canvasbacks (*Aythya valisineria*) (Serie et al. 1992).

Female body mass may further influence variation in PI and has been shown to influence incubation (Gloutney and Clark 1991, Yerkes 1998) and brood adoption or abandonment (Kehoe 1986) in ducks. Only one study, however, examined the relationship between female body mass and brood survival, but detected no relationship of these variables in Canvasbacks or Redheads (*Aythya americana*) (Arnold et al. 1995).

Brood movements among wetlands may affect brood survival and could be influenced by female age and body mass, although these have not been examined to date. Females may move their broods in response to low invertebrate numbers or to avoid wetlands lacking a zone of emergent vegetation. Results from studies examining the relationship between brood movements and brood survival are conflicting: some demonstrate a negative relationship (Rotella and Ratti 1992a), whereas others found a positive or no relationship (Mauser et al. 1994).

Little is known about Redhead brood survival or

¹ Received 22 July 1999. Accepted 4 April 2000.

² Current Address: Ducks Unlimited, Inc., Institute for Wetland and Waterfowl Research, One Waterfowl Way, Memphis, TN 38120-2351, e-mail: tyerkes@ducks.org

brood movements. Redheads are interesting because they frequently engage in nest parasitism prior to nesting. This behavior, known as a dual strategy (Sorenson 1990), may be energetically costly and therefore influence subsequent PI and brood success due to decreased body condition. Elsewhere I have demonstrated that Redheads exhibit lower PI, in the form of incubation constancy, compared to other ducks of similar body size (Yerkes 1998). Furthermore, among conspecifics, Redheads with lower body mass exhibit lower incubation constancy than heavier females (Yerkes 1998). These tendencies could ultimately result in decreased brood and duckling survival and subsequent recruitment in Redheads. Therefore the objectives of this study were first to document brood and duckling survival, the number of surviving ducklings, and brood movements. Secondly, the objectives were to determine how these parameters are affected by age and body mass of brood rearing females.

METHODS

I conducted this study in southwestern Manitoba (50°15'N, 99°50'W) in 1994 and 1995 (see Stoult 1982 for study site description). Habitat conditions were good for diving ducks in both years of this study. I trapped female Redheads on nests between 22 and 24 days of incubation, aged (Dane and Johnson 1975), weighed (± 5 g), and surgically implanted radio transmitters. Surgical procedures followed Korshgen et al. (1984).

I located females with broods daily with either a truck-mounted 2-antenna, 4-element system, or by 3-element hand held antennae. I counted daily the number of ducklings per brood or as often as they were sighted. On two occasions, ducklings were not counted because emergent cover restricted visibility. I monitored broods for a maximum of 30 days post-hatch or until all ducklings in a brood died.

A brood was considered successful if at least one duckling survived 30 days (Klett et al. 1986). Brood survival was determined as the proportion of broods that survived to 30 days. Duckling survival was estimated using a modified Mayfield method (Flint et al. 1995). Daily survival rates (DSR) for ducklings were estimated for two periods, <8 days and 8–30 days, because high mortality occurs early in brood rearing (Mauser et al. 1994, Guyn and Clark 1999). The 30-day survival estimate was the product of the survival estimates for the two periods (Johnson 1979). The last known number of ducklings was used as a measure of the number of surviving ducklings from a brood. I used this number as a relative comparison of brood size among females because one egg from each clutch was removed as a part of another study (Yerkes 1998).

I measured brood movements on aerial photographs as straight-line distances between the centers of wetlands used by broods. A brood movement was considered to have occurred only when a brood was observed on a new wetland or, in the case of 100% emergent cover, when a female remained on the wetland for at least three consecutive days. Occasionally, females left broods unattended and flew to nearby wetlands, but these movements were not considered.

DATA ANALYSIS

I examined the influence of female age, body mass, and hatch date on brood survival, duckling DSRs (<8 day, 8–30 day, and 30-day), and the number of ducklings with a general linear model (PROC GLM) (SAS Institute 1989) for main effects and possible interactions. I examined brood movements for possible correlation (PROC CORR) and compared movements between successful and unsuccessful females with *t*-tests (PROC TTEST). Because all brood movements were highly correlated, a backward stepwise discriminant analysis procedure (PROC STEPDISC) was used to determine which of the brood movement measures accounted for the most variability between successful and unsuccessful females. A general linear model (PROC GLM) was used to determine the influence of age and body mass on brood movements identified by discriminant analysis. Values reported are means \pm SE.

RESULTS

Forty broods were monitored from hatch to ≤ 30 days in 1994 ($n = 12$) and 1995 ($n = 28$). Brood survival was 55% ($n = 40$), and the average number of surviving ducklings was 4.2 ± 0.4 ($n = 36$, range 0 to 9). DSR for 30 days was 0.870, and DSR for older ducklings (8–30 day) (0.971 ± 0.054 , $n = 29$) was higher than younger ducklings (<8 day) (0.896 ± 0.035 , $n = 34$) ($\chi^2_1 = 19.4$, $P < 0.001$). Hatch dates ranged from 10 June to 21 July in 1994 and 18 June to 28 July in 1995, and were not significantly different between yearling ($n = 16$) and adult females ($n = 24$; $t_{38} = 0.6$, $P > 0.50$). Undetermined predators killed two females and two other broods could not be observed.

Only female body mass influenced brood survival in a model that examined the effect of age, body mass, and hatch date ($F_{1,39} = 5.2$, $P < 0.05$); although the overall fit of the model was low ($R^2 = 0.13$). All interactions in this model were insignificant and deleted from the model. Body mass of successful brood-rearing females (937.7 ± 12.3 g, range 840–1,090, $n = 22$) was higher than unsuccessful females (903 ± 11.5 g, range 810–990, $n = 18$). Body mass also was the only significant main effect in models examining the influence of age, body mass, and hatch date on duckling number ($F_{1,38} = 10.1$, $P < 0.01$), <8 day DSR ($F_{1,33} = 4.9$, $P < 0.05$), and 30 day DSR ($F_{1,34} = 4.0$, $P = 0.05$). Neither age, body mass, nor hatch date influenced 8–30 day DSR. Again, interactions were not detected. For successful females, the number of surviving ducklings tended to increase with increasing female body mass (Fig. 1a). The number of ducklings observed within one week of hatch was not correlated with female body mass ($r_s = 0.3$, $n = 38$, $P > 0.05$).

The average number of brood movements (2.5 ± 0.3 , range 0–9), distance of the first move (0.2 ± 0.03 km, range 0–0.7), longest distance moved (0.4 ± 0.04 km, range 1–1.1), and total distance moved (0.8 ± 0.1 km, range 0–3.6) were all positively and significantly correlated (all $r \geq 0.42$, all $P < 0.01$). All brood movements differed between successful and unsuccessful females. In backward stepwise discriminant analysis, the distance of the first move accounted for the most variation in survival ($R^2 = 0.08$, $F_{1,37} = 3.4$, $P > 0.07$),

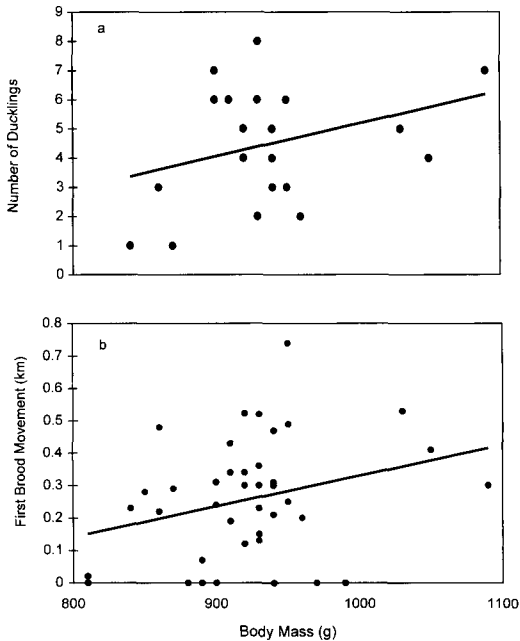


FIGURE 1. (a) Relationship between female body mass and number of surviving ducklings for successful brood rearing female Redheads ($n = 22$) and (b) relationship between distance of the first brood movement and body mass of female Redheads ($n = 40$). Solid lines represent the predicted relationships.

whereas no movement measures were significant in a similar model with number of ducklings as the dependent variable. In a full model with the distance of the first brood movement as the dependent variable, only body mass was significant ($F_{1,39} = 4.9$, $P < 0.05$). The distance of the first brood movement increased with female body mass at hatch (Fig. 1b).

DISCUSSION

Redhead brood and duckling survival are associated with female body mass and brood movements, but not female age or hatch date. In Redheads, post-hatch PI may be influenced by pre-hatch reproductive effort, therefore age may be a complicating factor due to the parasitic tendencies of this species. Sorenson (1990) demonstrated that older females were more likely to invest in a dual reproductive strategy, which may be more energetically costly. Reproductive strategy choice may further be influenced by body mass (Sorenson 1990, Yerkes and Koops 1999), such that older, heavier females may invest more in pre-hatch reproductive effort and begin brood rearing at weights similar to females that only nested. Therefore, due to the variety of reproductive strategies available to Redheads, older females may invest heavily in pre-hatch reproductive costs and may not exhibit the age-related brood survival that has been observed in other duck species (Blums et al. 1997).

Studies on Mallards (*Anas platyrhynchos*) (Mausser

et al. 1994), Buffleheads (*Bucephala albeola*) (Savard et al. 1991), and now Redheads, found no relationship between hatch date and brood survival. Others, however, have documented lower survival of late-hatched broods (Rotella and Ratti 1992b, Guyn and Clark 1999). This relationship is sometimes associated with younger females nesting later in the season, but this explanation cannot apply to Redheads in this study, nor in Sorenson's (1990), because adult and yearling hatch dates were not significantly different.

Females that were heavier at the end of incubation had higher brood survival and produced more ducklings per brood than lighter females. This result is not due to heavier females initially producing more eggs and thus hatching more ducklings because I did not detect a relationship between body mass at the end of incubation and the number of ducklings that hatched. My results contrast with those of Arnold et al. (1995) who demonstrated that late incubation body mass was unrelated to brood and duckling survival in Redheads and Canvasbacks. It may be that females in better condition at the end of incubation devote more time to brood care activities than females that weigh less. Lighter females may be required to devote a significant amount of brood rearing time to self maintenance, particularly during the early part of brood rearing (<8 days) when body mass significantly influenced duckling daily survival rates. No time budget studies have been reported for females in varying body condition states during brood rearing. One study, however, illustrated that brood rearing females devote about 50% of their time to self maintenance (mostly feeding) and that females with broods spend less time feeding than females without broods (Afton 1984). Body condition likely influences amount of time spent feeding by females during brood rearing especially during the time immediately following hatch when female body mass is lower than any other time of the year (Alisauskas and Ankney 1992).

My results suggest that brood movements are important to Redhead brood survival. Brood movements are common among ducks and often influence brood survival. Typically, the greatest distances moved by ducklings occur within the first week post-hatch (Rotella and Ratti 1992a); a finding similar for Redheads in this study given that the first distance moved was often the longest. In Mallards, brood movement distances were negatively correlated with survival (Rotella and Ratti 1992b). For broods moving shorter distances, median duckling survival was higher (Rotella and Ratti 1992b). In contrast, some studies did not detect a relationship between survival and overland movements by broods (Mausser et al. 1994).

Measures of brood movements differed between successful and unsuccessful female Redheads: successful females moved more often, made longer first moves, executed longer moves in general, and moved greater total distances than unsuccessful females. Total number and distance of movements are probably greater by virtue of the broods of successful females surviving more days than those of unsuccessful females; however, distance of the first brood movement was an important factor influencing survival. The influence of brood movements on brood survival is equivocal. For

example, movements of Mallard broods were negatively correlated with survival and the number of ducklings that survived (Rotella and Ratti 1992b), but I detected the opposite relationship in Redheads in which the first distance moved enhanced brood survival. This pattern may reflect a strong preference for specific types (Yerkes, in press) or conditions of wetlands by Redheads even though it requires longer overland movements to reach them, thus potentially suggesting that Redheads may have more specialized habitat requirements than Mallards. Additionally, body mass is associated with movements, although female age is not. Females that are heavier at the end of incubation traveled farther during the first brood movement than lighter females. Again, this may reflect preference for specific wetlands and the ability to reach them by virtue of better body condition.

R. Saylor and B. Davis provided helpful editorial comments. I thank the numerous field assistants that helped collect data, especially S. Badzinski, J. Leo, M. Brasher, N. Dion, M. Gendron, B. Mense, G. Peroff, C. Reinke, and A. Selle. This research was funded by the Delta Waterfowl Foundation.

LITERATURE CITED

- AFTON, A. D. 1984. Influence of age and time on reproductive performance of female Lesser Scaup. *Auk* 101:255-265.
- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl, p. 30-61. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [EDS.], *Ecology and management of breeding waterfowl*. Univ. Minnesota Press, Minneapolis, MN.
- ARNOLD, T. W., M. G. ANDERSON, R. B. EMERY, M. D. SORENSON, AND C. N. DESOBRINO. 1995. The effect of late-incubation body mass on reproductive success of Canvasbacks and Redheads. *Condor* 97:953-962.
- BLUMS, P., G. R. HEPP, AND A. MEDNIS. 1997. Age-specific reproduction in three species of European ducks. *Auk* 114:737-747.
- DANE, C. W., AND D. H. JOHNSON. 1975. Age determination of female Redhead ducks. *J. Wildl. Manage.* 39:256-263.
- FLINT, P. L., K. H. POLLOCK, D. THOMAS, AND J. S. SEDINGER. 1995. Estimating pre fledging survival: allowing for brood mixing and dependence among brood mates. *J. Wildl. Manage.* 59:448-455.
- GLOUTNEY, M. L., AND R. G. CLARK. 1991. The significance of body mass to female dabbling ducks during late incubation. *Condor* 93:811-816.
- GUYN, K. L., AND R. G. CLARK. 1999. Factors affecting survival of Northern Pintail ducklings in Alberta. *Condor* 101:369-377.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- KEHOE, F. P. 1986. The adaptive significance of creching behavior in the White-winged Scoter. M.Sc. thesis, Univ. Guelph, Ontario, Canada.
- KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, AND K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U.S. Fish and Wildl. Serv. Resour. Publ. 158, Washington, DC.
- KORSHGEN, C. E., S. J. MAXSON, AND V. B. KUECHLE. 1984. Evaluation of implanted transmitters in ducks. *J. Wildl. Manage.* 48:982-987.
- MAUSER, D. M., R. L. JARVIS, AND D. S. GILMER. 1994. Survival of radio-marked Mallard ducklings in northeastern California. *J. Wildl. Manage.* 58:82-87.
- ROTELLA, J. J., AND J. T. RATTI. 1992a. Mallard brood movements and wetland selection in southwestern Manitoba. *J. Wildl. Manage.* 56:508-515.
- ROTELLA, J. J., AND J. T. RATTI. 1992b. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. *J. Wildl. Manage.* 56:499-507.
- SAS INSTITUTE INC. 1989. SAS/STAT user's guide, Version 6, 4th ed. SAS Institute, Inc., Cary, NC.
- SAVARD, J. L., G. E. JOHN SMITH, AND J. N. M. SMITH. 1991. Duckling mortality in Barrow's Goldeneye and Bufflehead broods. *Auk* 108:568-577.
- SERIE, J. R., D. L. TRAUGER, AND J. E. AUSTIN. 1992. Influence of age and selected environmental factors on reproductive performance of Canvasbacks. *J. Wildl. Manage.* 56:546-556.
- SORENSON, M. D. 1990. Parasitic egg laying in Redhead and Canvasback ducks. Ph.D. diss., Univ. Minnesota, Minneapolis, MN.
- STOUDT, J. H. 1982. Habitat use and productivity of Canvasbacks in southwestern Manitoba, 1961-1972. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Wildl. No. 248, Washington, DC.
- TALENT, L. G., R. L. JARVIS, AND G. L. KRAPU. 1983. Survival of Mallard broods in south-central North Dakota. *Condor* 85:74-78.
- TRIVERS, R. L. 1974. Parent-offspring conflict. *Am. Zool.* 14:249-264.
- YERKES, T. 1998. The influence of female age, body mass, and ambient conditions on Redhead incubation constancy. *Condor* 100:62-68.
- YERKES, T. In press. Nest site characteristics and brood habitat selection of Redheads: an association between wetland characteristics and success. *Wetlands*.
- YERKES, T., AND M. A. KOOPS. 1999. Redhead reproductive strategy choices: a dynamic state variable model. *Behav. Ecol.* 10:30-40.